NECTAR ROBBER PREFERENCE AND NECTAR AVAILABILITY IN FOUR HUMMINGBIRD POLLINATED FLOWERS

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Abstract. The mutualistic system which exists between hummingbird-pollinated flowers and their pollinators is parasitized in some areas by the slaty flowerpiercer and the fiery-throated hummingbird, which extract nectar without pollinating the flower in the process. The slaty flowerpiercer exhibits trap-lining behavior and the fiery-throated exhibits territorial behavior, while both may experience interspecific competition with non-thieving hummingbirds. Also, the nectar robbers may or may not be able to select patches of flowers on the basis of nectar availability. These interactions may alter behavior that would otherwise maximize foraging success. We hypothesized that in various hummingbird-pollinated flowers in the Cerro de la Muerte high elevation forest, the percentage of robbed flowers in a patch would increase as both patch size and nectar availability increased. Our results support this, suggesting that the nectar robbers are able to select the most beneficial patches and flower species, despite the presence of other territorial species occupying these patches. To address nectar availability, we hypothesized that flowers refill their nectar reservoirs at night. We found that not all flowers refill their nectar reservoirs and that refilling occurs mostly during the day. Thus, hummingbird and nectar robber activity should continue throughout the day rather than be restricted to early morning activity.

INTRODUCTION

Hummingbird flowers and their pollinators are prominent features of the forest edges of Cerro de la Muerte, Costa Rica. In the area adjacent to Albergue Cuerici Biological Research Station, many species of hummingbirds are present, among them *Colibri thalassinus* (green violet-ear), *Panterpe insignis* (fiery-throated), and *Eugenes fulgens* (magnificent). Many species of hummingbird flowers are also present, but four are common, including *Centropogon valerii*, *C. talamancensis*, *Bomarea* spp. and a species of Gesneriaceae. The nectar-thief specialist is a Coerebid bird, *Diglossa plumbea*, the slaty flowerpiercer.

Each bird species appears to have its preferred flower or flowers within this system. Colwell (1973) states that the magnificent pollinates each of the plant species listed above, while the green violet-ear specializes on *C. valerii*. The fiery-throated hummingbird is able to pollinate all the flowers except *C. talamancensis*, from which it steals nectar by puncturing the base of the flower. With its hooked beak, *D. plumbea* can pierce all of these flower species and remove nectar without pollination.

The fiery-throated hummingbird is territorial while the slaty flowerpiercer exhibits trap-lining behavior between dense resource patches (Colwell 1973). It has not been shown, however, whether these two species selectively steal nectar, discriminating between patches on the basis of patch size and flower species. In the presence of interspecific competition with a territorial hummingbird (i.e., the magnificent), the fiery-throated or the slaty flowerpiercer may be displaced entirely, or chased away from patches, regardless of patch size, or quality. If these nectar robbers are being expelled after only a short intrusion, they should only be able to rob a few flowers, regardless of patch size. These nectar thieves may also be forced to forage in non-preferred patch sizes. To examine whether nectar robbers are able to forage in the most productive patches, we tested the hypothesis that nectar thieving should be positively related to patch size and quality. This assumes that these species are unconstrained by local intra- or interspecific territorial species.

To maximize foraging success, both the trap-lining and territorial species would also need to know when the flowers refill their nectar. For the two *Centropogon* flower species, Colwell (1973) stated that flowers produce nectar throughout their 8-12 day life span, but it was not clear whether all flowers contained nectar nor when they replenish their nectar reservoirs. Based on Colwell's findings, we predicted that all flowers in a patch of *Centropogon valerii* and *C. talamancensis* should contain nectar. We also predicted that this nectar production would occur at night, and thus nectar volumes would be higher in the morning than in the afternoon.

METHODS

We sampled one patch of *Centropogon valerii*, four patches of *C. talamancensis*, six patches of *Bomarea* sp., and one patch of a species of Gesneriaceae along various trails of the station. We defined a patch as a group of flowers in which no flower was greater 0.5 m from its nearest neighbor. Patches ranged from a very tight cluster of about 30 flowers in one individual of *Bomarea* sp. to a 4 m x 2 m patch of *C. talamancensis*. Only patches near the road or trail and only flowers < 2 m tall were included. We sampled 408 mature, unwilted flowers of these four species and recorded the presence or absence of thieving punctures in the corolla of each flower.

To determine nectar availability in two species of *Centropogon*, we examined the presence or absence of nectar in each flower within a patch. The amount of nectar was measured with 20 µl pipettes, and placed in two categories, high (> 5 µl) or low (≤ 5 µl). To estimate overnight nectar production we bagged 20 flowers in each patch in the afternoon (1400-1600). We returned the next day and measured nectar quantities in early morning (0700 - 0900), and again in the afternoon (1400 - 1600).

For statistical analysis, proportions were arcsin transformed to meet the assumption of normality.

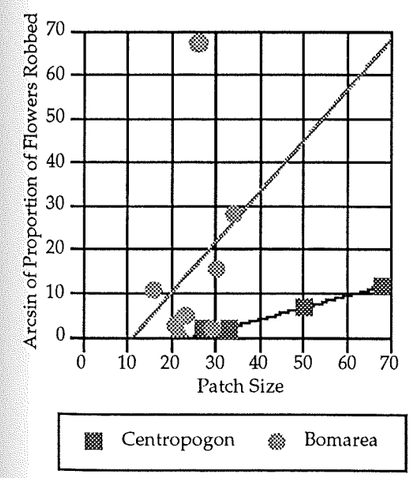

FIG. 1. Arcsin of proportion of flowers robbed vs. patch size. (*Centropogon*, n=5, *Bomarea*, n=6)

RESULTS

The proportion of flowers robbed increased with total number of flowers per patch (patch size) for the two *Centropogon* species combined (R^2=0.836, df=1,4, P=0.01, Fig. 1). There was a similar trend for the Bomarea sp. (R^2=0.609, df=1,6, P=0.02, Fig. 1). We could not determine if this trend held for the Gesneriaceae because of our small sample of this flower species. All flowers sampled were grouped together for

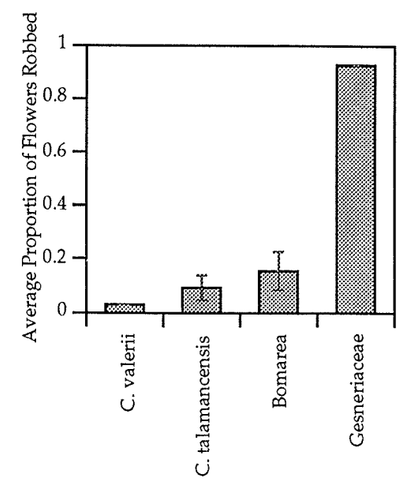

FIG. 2. Mean percent of flowers robbed by species (*C. valerii*, N=33 in 1 patch; *C. talamancensis*, N=174 in 4 patches; *Bomarea*, N=175 in 6 patches; Gesneriaceae, N=26 in 1 patch).

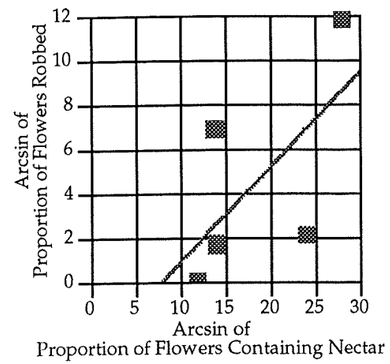

FIG. 3. Arcsin of proportion of flowers robbed vs. arcsin of proportion of flowers containing nectar in *Centropogon valerii* and *C. talamancensis* (n=207 in 5 patches).

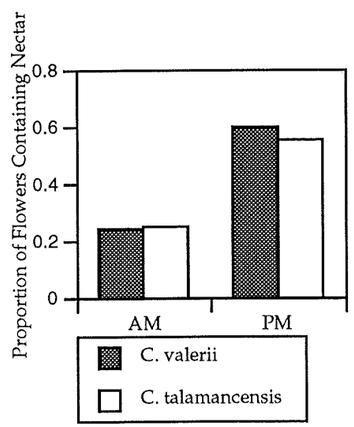

FIG. 4. Differential nectar production in two species of *Centropogon* as a function of time of day (*C. valerii* 0700-0900, N=33; 1400-1600, N=20; *C. talamancensis* 0700-0900, N=68; 1400-1600, N=20).

each regression regardless of number of patches sampled.

In addition to these associations between patch size and proportion of flowers robbed, we found a difference between species for average proportion robbed. The *Centropogon* species showed the lowest proportion of flowers robbed, while more than 90% of the Gesneriaceae flowers were robbed (Fig. 2).

We found a positive reletionship between the proportion of flowers robbed and the proportion of flowers containing nectar per patch (R^2=0.683, df=1,4, P=0.04, Fig. 3) for the two *Centropogon* species.

There was also a significant association between proportion of *Centropogon* flowers with nectar and time of day. The proportion of flowers with nectar was significantly higher during the day than at night in both *C. valerii* (X^2=6.8, df=1, P=0.009, Fig. 4) and *C. talamancensis*, (X^2=10.0, df=1, P=0.002, Fig. 4). Neither *Centropogon* species produced nectar in all flowers (Fig. 4).

DISCUSSION

Our results support the hypothesis that the percentage of flowers robbed per patch increases as patch size and nectar availability increase. Therefore, nectar robbers at Cerro de la Muerte seem able to select and use the largest and most beneficial patches, as measured by nectar availability, despite the presence of potential intra- and inter-specific competition. This implies that competition either does not exist or that these nectar robbers are able to avoid it.

Some flower species, such as the Gesneriaceae, are preferentially robbed, though all species exhibited some robbery effects. This differential robbing could be due to increased nectar production, absence of an aggressively defending hummingbird, ability of a robber to steal from a given flower and overall flower availability. In order to understand the selection made by these nectar robbers, it would be important to quantify and compare the above factors.

Nectar appears to be produced predominantly during the daytime. This may be a reason for the general observation that hummingbirds are active throughout the day rather than only in the morning hours. The same effect should be observed in nectar thieves.

Because not all flowers produce nectar at any given time, the proportion of flowers with nectar in a patch does not remain constant. Therefore, a visual assessment of patch size is not sufficient to measure nectar availability unless production rates are

known for that species. We would expect hummingbird and nectar robber territory size to increase with decreased nectar availability within a patch. A longer term study that measures total nectar production per species per flower lifetime is needed to accurately quantify the effects of nectar production on hummingbird activity.

LITERATURE CITED

Colwell, R. K., B.J. Betts, P. Bunnell, F.L. Carpenter, and P. Feinsinger. 1974. Competition for the nectar of *Centropogon valerii* by the hummingbird *Colibri thalassinus* and the flowerpiercer *Diglossa plumbea*, and its evolutionary significance. Condor 76:447-489.

Colwell, R.K. 1973. Competition and coexistence in a simple tropical community. American Naturalist 107: 737-759.